Survival Strategy of the Terricolous Millipede *Cutervodesmus adisi* Golovatch (Fuhrmannodesmidae, Polydesmida) in a Blackwater Inundation Forest of Central Amazonia (Brazil) in Response to the Flood Pulse

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ABSTRACT

Reaction of *Cutervodesmus adisi* Golovatch, 1992 to 5-7 months of flooding was studied in 1976/77 and 1983/84 in a blackwater inundation forest near Manaus, Brazil. The study area was annually covered by several metres of floodwater, due to the monomodal flood pulse of the Rio Negro. Juvenile migratory stages with 18 (and 17) segments spent the inundation period on tree trunks. In 1976/77, they represented 42% of all Polydesmida caught in arboreal traps on 6 tree trunks over a period of 18 months (n = 5661). After flooding, the migratory stages of *C. adisi* recolonized the forest floor. They developed to adults which subsequently reproduced. Vertical distribution of 94% of all animals extracted from 0-14 cm soil depth was restricted to the upper 7 cm. Migratory stages of the offspring moved into tree trunks. Trunk ascents began several weeks before forest inundation and after the rainy season had started. Trunk ascents and descents, as well as the vertical distribution of *C. adisi* in the soil during the non-inundation period, are discussed with respect to abiotic factors in the study area (precipitation, insolation, temperature and humidity of soil and air) as well as macroclimatic influences (El Niño events). *C. adisi* is considered to be an endemic species of the blackwater inundation forests in the Rio Negro Valley. Vertical migration of its juvenile stages represents an ethological adaptation to escape annual long-term flooding, which was not found in Polydesmida of neighbouring non-flooded upland forests.

RÉSUMÉ

Stratégie de survie du diplopode terricole *Cutervodesmus adisi* Golovatch (Fuhrmannodesmidae, Polydesmida) dans une forêt inondable de l'Amazonie centrale en réponse à la fréquence des inondations.

Les réactions de *Cutervodesmus adisi* Golovatch, 1992 à une période de 5 à 7 mois d'inondation ont été étudiées en 1976/77 et 1983/84 dans une forêt inondable d'eau noire près de Manaus au Brésil. Le site d'étude est annuellement recouvert par plusieurs mètres d'eau, consécutivemement au flux d'inondation monomodal du Rio Negro. Les stades juvéniles migrateurs à 18 (et 17) anneaux passent la période d'inondation dans les troncs d'arbres. En 1976/77, ils

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Source : MNHN, Paris

représentaient 42% de tous les Polydesmida capturés dans les pièges arboricoles relevés sur six troncs d'arbres durant 18 mois (n = 5661). Après l'inondation, les stades migrateurs de *C. adisi* ont recolonisé le sol forestier. Ils se sont développés en adultes qui se sont ensuite reproduits. La répartition verticale de 94% de tous les individus extraits d'une épaisseur de sol de 14 cm se réduit aux 7 cm supérieurs. Les stades migrateurs issus du recrutement annuel se déplacent sur les troncs d'arbres. L'ascension du tronc commence plusieurs semaines avant l'inondation de la forêt et après le démarrage de la saison des pluies. L'ascension et la descente le long des troncs, de même que la répartition verticale de *C. adisi* dans le sol en dehors de la période d'inondation, sont discutées en rapport avec les facteurs abiotiques du site d'étude (précipitation, insolation, température, humidité de l'air et du sol) ainsi qu'avec les influences macroclimatiques (évènements dûs au El Niño). *C. adisi* est considéré comme une espèce endémique des forêts inondables de la vallée du Rio Negro. La migration verticale de ses stades juvéniles représente une adaptation éthologique lui permettant d'échapper à une inondation à long terme, comportement qu'on ne retrouve pas chez les polydesmides des forêts non-inondées plus élevées.

INTRODUCTION

Terrestrial invertebrates in periodically flooded ecosystems require special "survival strategies" (cf. ADIS, 1992a). In Central Amazonia, the monomodal "flood pulse" (JUNK *et al.*, 1989) of the Rio Negro and the Rio Solimões-Amazon causes flooding of forests near rivers - the so-called seasonal inundation forests (PRANCE, 1979) - and their adjacent shores by several metres of floodwater for 5-7 months each year. Terrestrial invertebrates have adapted to this ecosystem. The fauna comprises terricolous and arboricolous animals. Both groups include non-migrants and migrants. Migratory reaction of terricolous animals is horizontal (following the high water line), vertical (temporal ascent to trunk or canopy) or includes a temporal flight to upland forests. Non-migrants have active or dormant stages under water. The latter pass inundation in naturally available retreats, in self-made retreats or as eggs. Non-migrant arboricolous animals reproduce and live exclusively in the trunk and canopy region, whereas migrants include life stages that live on the ground as well. Characteristics and examples of species for each of these categories are given by ADIS (1992a, b).

In the vicinity of Manaus, millipedes alone display a good variety of responses to seasonal floods. Thus, *Gonographis adisi* Hoffman, 1985 (Pyrgodesmidae, Polydesmida) appears to be unique in being the only hitherto known millipede capable of surviving submersion for up to 11 months due to a hydrophobic secretion layer on the cuticula which enables plastron respiration (HOFFMAN, 1985; ADIS, 1986; MESSNER & ADIS, 1988). On the contrary the even more widespread synanthropic *Muyudesmus obliteratus* Kraus, 1960 (Pyrgodesmidae), another forest floor-dweller, escapes flooding by moving to the non-inundated tree trunks and canopy areas (like most other millipedes); its plastron is incomplete thus long-term submersion is fatal (ADIS, 1986; MESSNER & ADIS, 1988). *Mestosoma hylaeicum* Jeekel, 1963 (Paradoxosomatidae, Polydesmida) generally displays the same pattern of behaviour, with all the phases of its life-history neatly corresponding to local seasonality (ADIS, 1992c). Probably the same holds true for *Prostemmiulus adisi* Mauriès, 1984 (Stemmiulidae, Stemmiulida), perhaps the only one of three congeners (the others being *P. amazonicus* Mauriès, 1984, and *P. wellingtoni* Mauriès, 1984) encountered in inundation forests that shows similar seasonal vertical migrations from the forest floor to the trunk/canopy areas and back (MAURIÈS, 1984). The same can obviously be said about *Moojenodesmus pumilus* Schubart, 1944, *M. susannae* Golovatch, 1992 (Fuhrmannodesmidae, Polydesmida) (GOLOVATCH, 1992a) and *Onciurosoma adisi* Golovatch, 1992 (Paradoxosomatidae) (GOLOVATCH, 1992b).

Another different survival strategy is demonstrated by *Epinannolene arborea* Hoffman, 1984 (Pseudonannolenidae, Spirostreptida), obviously a strict arboricole (HOFFMAN, 1984; ADIS, 1984) which remains in the upper trunk and canopy region unless forced down the trunk by insolation/drought when it retreats under the bark and estivates there.

In this paper, adaptive reaction of the diplopod *Cutervodesmus adisi* Golovatch, 1992 from a seasonal blackwater inundation forest in the Rio Negro valley to the annual flooding is

Source : MNHN, Paris

discussed. Its survival strategy is compared with that of Diplopoda already known to inhabit inundation forests in the surroundings of Manaus.

STUDY AREA AND METHODS

Diplopoda were collected between 1975 and 1988 in the course of ecological studies on terrestrial invertebrates from Central Amazonian floodplains, in particular the seasonal inundation forests (cf. ADIS, 1981, 1984, 1992 a-c; ADIS & SCHUBART, 1984).

The study site was situated on the lower course of the Rio Tarumã Mirím (03°02'S, 60°17'W), a tributary of the Rio Negro, about 20 km upstream from Manaus. The seasonal blackwater inundation forest (for definition see PRANCE, 1979) was situated on a slope and extended from the non-inundated dryland area (= upland or terra firme) with a constant decline (< 5%) to the bare sandy shoreline of the Rio Tarumã Mirím (see profile in BECK, 1976). The central part of the study site was covered annually by up to 3.35 m of floodwater between March/April and August/September. Further information on the study site is given by ADIS (1981, 1984, 1992a), MEYER (1991) and WORBES (1986).

The activity density of Diplopoda evaluated in this study was monitored on the forest floor with 8 ground photo-eclectors of FUNKE (= emergence traps) during the non-inundation period in 1976/77. Trunk ascents and descents were detected at weekly or bi-weekly intervals with arboreal photo-eclectors (= funnel traps) on three tree trunks each of the dominant tree species (cf. Table 1) between December 1975 and May 1977. The killing/preserving agent used in all traps was aqueous picric acid solution (without detergent), which is known to be mostly neutral in terms of attraction or repellence in temperate zones (ADIS, 1979). All capture devices are fully described by ADIS (1981) and FUNKE (1971), who also explain their mode of utilization and function. Trunk ascents of Diplopoda and their activity on the ground were additionally monitored with funnel traps on one tree and with 1-4 emergence traps on the forest floor during the non-inundation periods in 1982/83 and 1983/84, respectively.

Distribution of Diplopoda in the non-flooded soil was studied between September, 1981 and February, 1982. Once a month, six soil samples were taken at random along a transect with a split corer (= steel cylinder with lateral hinges; diameter 21 cm, length 33 cm) which was driven into the soil by a mallet. Each sample of 14 cm depth was then subdivided into four subsamples of 3.5 cm each. Animals were extracted from subsamples following a modified method of KEMPSON (ADIS, 1987).

The presence of Diplopoda in the flooded soil was studied at the end of each inundation period in 1984-88. Twelve soil samples were taken at 3-weekly intervals under water as described above. Each of the subsamples was kept moist for 10-14 days on a grid inside a bucket, which was covered by a cotton screen (sealed up by a plastic snap ring) and contained aqueous picric acid in the bottom. Animals were subsequently extracted with the modified KEMPSON apparatus.

The presence of Diplopoda in tree crowns was tested by fogging canopies with pyrethrum in the early dry season (July 1977, 1979), when the inundation forest was completely flooded (cf. ADIS *et al.* 1984; ERWIN, 1983). Bromeliads, 5-25 m above ground, were also sampled and checked for terrestrial invertebrates in August, 1979 (forest not flooded) and June, 1981 (forest flooded).

Seasonal inundation forests in Central Amazonia are subject to a rainy season (December - May: average precipitation 1550 mm), and a "dry" season (June - November: average precipitation 550 mm, but each month has some rain events; cf. RIBEIRO & ADIS, 1984). Vertical distribution of Diplopoda in relation to changing conditions of soil moisture content, temperature and pH, was statistically evaluated with the linear correlation test (CAVALLI-SFORZA, 1972), using the original field data. This method was also used to evaluate the activity of Diplopoda on the soil surface and tree trunks in relation to insolation, precipitation, temperature and humidity of the air.

The taxonomic work for this paper was done by S. I. GOLOVATCH (cf. GOLOVATCH, 1992a, b), the evaluation of field data by J. ADIS and S. HAMANN. Diplopoda sampled were classified as juveniles (7, 9, 12, 15, 17 and 18 pairs of legs), subadults (19 pairs of legs) and adults (20 pairs of legs) according to SCHUBART (1934). Sex was determined in the adults.

RESULTS AND DISCUSSION

About 2600 specimens of *Cutervodesmus adisi* Golovatch, 1992 were collected in the seasonal blackwater inundation forest under study. Of these, 98% could be grouped into developmental stages. The majority were juveniles (97.1% of the total catch; n = 2420), 1.7% were subadults (n = 43) and 1.2% adults (n = 29).

C. adisi represented 60.4% (329 ind. m^{-2} $month^{-1}$) of all Diplopoda (545 ind. m^{-2} $month^{-1}$) extracted from soil samples during the non-inundation period 1981/82. A total of 7.2 ± 4.0 millipedes per m^2 (1.4 ind. m^{-2} $month^{-1}$) were collected on the soil surface during the non-inundation period in 1976/77. Animals occurred solely from January to April (rainy season) in ground photo-eclectors and were not detected during the preceding dry season. Out of these, *C. adisi* represented 4.5 ± 0.7 ind. m^{-2} (= 62.5 %; 0.9 ind. m^{-2} $month^{-1}$). The majority of the total diplopods obtained in 1976/77 was sampled on tree trunks (cf. Table 5 *in* ADIS, 1981): out of

Source : MNHN, Paris

the 13516 specimens caught, 17.5% (n = 2369) were represented by *C. adisi*. It was the eudominant species of all Polydesmida collected (n = 566l) and represented 41.9% of their total catch. The percentage of trunk ascending individuals of *C. adisi* was higher (28.2% of the total Diplopoda and 66.7% of all Polydesmida caught), when compared to trunk descending animals (15.1% of the total Diplopoda and 36.1% of all Polydesmida sampled).

C. adisi reaches 6.0 mm in length (cf. GOLOVATCH, 1992a). The species is considered hemiedaphic, as 94% of all specimens extracted from soil samples in 1981/82 were found in the top 7 cm (Fig. 1), independent of seasons. This becomes evident, when significant correlations between the abundance of *C. adisi* and different soil conditions in the study area are carefully analysed.

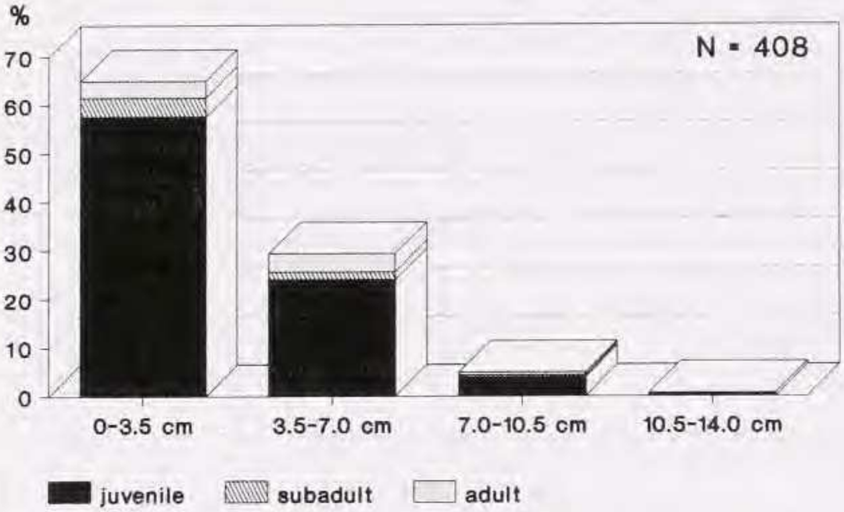

FIG. 1. — Distribution of developmental stages of *Cutervodesmus adisi* in the soil at Rio Tarumã Mirím. Monthly samples taken every 3.5 cm to a depth of 14 cm between September, 1981 and February, 1982 (non-inundation period); total catch = 100%.

During the dry season the decreasing abundance with greater soil depth was positively correlated with the increasing soil moisture content (e.g. Nov. 19, 1981: $p < 0.01$, $r = +0.9924$ for the total catch and $p < 0.05$, $r = +0.9798$ for juveniles; $n = 4$, respectively). However, during the rainy season, particularly after heavy rainfalls, the decreasing abundance was negatively correlated with the now decreasing soil moisture content in greater soil depth (e.g. Dec. 17, 1981: $p < 0.001$, $r = -0.9995$ for juveniles; $n = 4$). Similar changes were found with regard to soil temperatures: an increase with greater soil depth after heavy rainfalls was negatively correlated with the decreasing abundance of *C. adisi* ($p < 0.05$), whereas a temperature decrease with greater soil depth during dryer periods was positively correlated with the decreasing abundance of the species ($p < 0.05$).

Grain size and mineral composition of the soil seem to be especially important for the vertical distribution of terricolous arthropods in seasonal inundation forests (cf. ADIS *et al.*, this volume). First analyses of soil data (ADIS & IRION, unpubl.) indicated, that the decreasing abundance of *C. adisi* with greater soil depth during the dry and rainy seasons corresponded with an increasing amount of grains > 1000 µm in lower soil layers (from 0.7% in 0-3.5 cm to 2.7% in 10.5-14 cm depth; $p < 0.05$) and with a decreasing amount of silt from 14.6% in the top 3.5 cm to 10.8% in 14 cm soil depth ($p < 0.05$).

During the rainy season the decreasing abundance of *C. adisi* was negatively correlated with the increasing pH in lower soil layers as well ($p < 0.05$).

About 85% of the *C. adisi* population extracted from soil samples in 1981/82 was represented by juveniles, 7% by subadults and 8% by adults (Fig. 2). The sex ratio of males and females was 1:1.5 (n = 27). Adults and early larval stages (7, 9 & 12 segments) occurred solely in the soil (Fig. 3) where reproduction must have taken place.

Source : MNHN, Paris

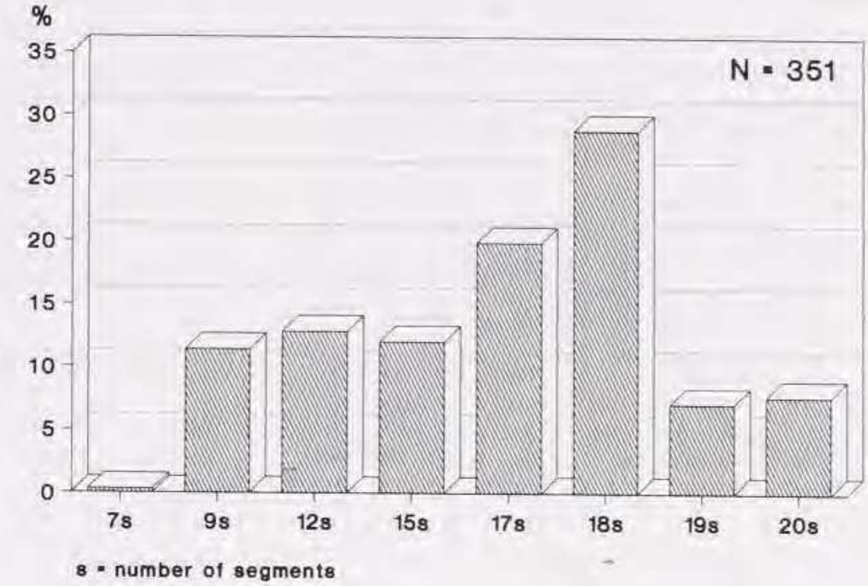

FIG. 2. — Percentage of developmental stages of *C. adisi* caught in the soil (0-14 cm depth). Monthly samples taken between September, 1981 and February, 1982 (non-inundation period) at Rio Tarumã Mirím.

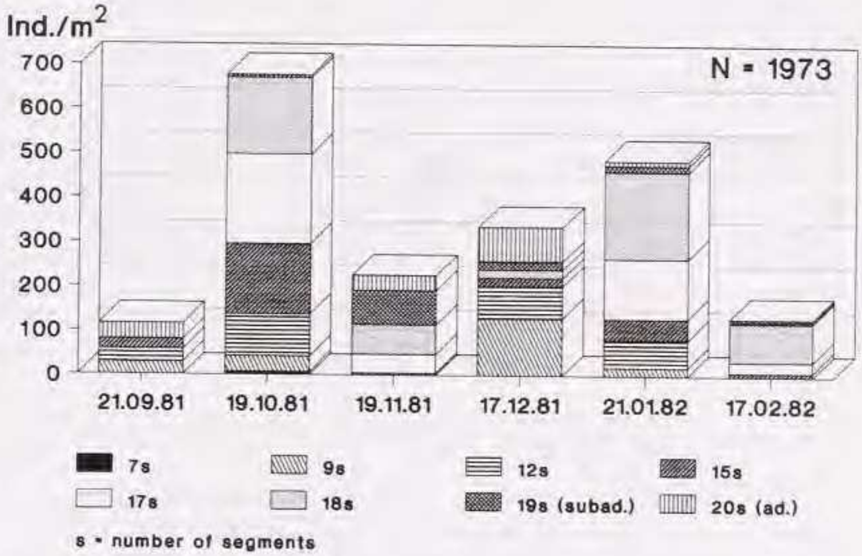

FIG. 3. —Temporal occurrence and abundance of *C. adisi* (ind./m2) in the soil (0-14 cm depth). Monthly samples taken between September, 1981 and February, 1982 (non-inundation period) at Rio Tarumã Mirím.

Advanced juvenile stages (the majority with 18 segments, some with 17 segments; cf. Table 1) were found to pass the inundation period in the trunk region (Figs 4, 5) and to recolonize the forest floor after the floodwater had receded. In 1981, some animals had already moulted to adults and reproduced within the first five weeks after the forest floor had dried, as juvenile stages of the offspring occurred from mid-September onwards (Fig. 3). Abundance of *C. adisi* in the soil was highest during the dry season (October 19, 1981: 678 ind. m^{-2}). The first larval stage of the progeny (7 segments, 3 pairs of legs) was obtained at this time only and is believed to be of short duration (cf. HOPKIN & READ, 1992). In 1981/82, 49% of all *C. adisi* specimens extracted from soil samples comprised advanced juvenile stages with 18 segments and to a lesser extent with 17 segments (Fig. 2). They represented "migratory stages" which came to the soil surface at the beginning rainy season and started ascending tree trunks (Fig. 4).

Source : MNHN, Paris

In 1976, they were caught in ground photo-eclectors from January onwards, and activity density became greater with an increasing water saturation of the soil during subsequent weeks ($p < 0.05$, $r = +0.521$; $n = 16$; Fig. 4). Shortly before forest inundation, abundance of *C. adisi* in the soil was lowest (131 ind. m^{-2}; Fig. 3). The juveniles of non-migrating stages remaining in the soil were forced into the trunk area by the inundation of the forest (Table 1). Similar behaviour was found in two species of pseudoscorpions, and where tritonymphs represented the migratory stage (ADIS & MAHNERT, 1985; ADIS *et al.*, 1988).

TABLE 1.— Number (ind.) and dominance (%) of developmental stages of *Cutervodesmus adisi* caught during trunk ascents (BE↑) and trunk descents (BE↓) on three different tree species of Leguminosae in different years (capture periods: BE↑ from December to May in 1975/76, 1976/77, 1982/83 & 1983/84; BE↓ from July to October, 1976). No specimens were captured on *Mora paraensis* DUCKE (Caesalpiniaceae) between July and October, 1976. N.I. = No Investigation.

Trunk ascent (BE ↑)	Stage	1975/1976	1976/1977	1982/1983	1983/1984	Total	
		N	N	N	N	N	%
Aldina latifolia Benth var. *latifolia* I (Fabaceae)	15	–	–	1	–	1	1.1
	17	–	–	5	3	8	8.4
	18	3	3	14	52	72	75.8
	19	–	–	13	1	14	14.7
	Total	3	3	33	56	95	100.0
Aldina latifolia Benth var. *latifolia* II (Fabaceae)	17	–	14	N.I.	N.I.	14	2.7
	18	29	476			505	97.3
	Total	29	490			519	100.0
Peltogyne venosa Benth ss. *densiflora* (Benth) M. Silva (Caesalpiniaceae)	17	1	1	N.I.	N.I.	2	1.2
	18	25	138			163	98.8
	Total	26	139			165	100.0

Trunk descent (BE↓)	Stage	1976		SUM	Trunk ascent		Trunk descent		Total	
		N	%	Stage	N	%	N	%	N	%
Aldina latifolia Benth var. *latifolia* III (Fabaceae)	17	252	23.1	15	1	0.1	–	–	1	0.1
	18	837	76.9							
	Total	1089	100.0	17	24	3.1	273	20.5	297	14.1
Aldina latifolia Benth var. *latifolia* IV (Fabaceae)	17	21	8.7	18	740	95.0	1057	79.5	1797	85.2
	18	220	91.3	19	14	1.8	–	–	14	0.7
	Total	241	100.0	Total	779	100.0	1330	100.0	2109	100.0

In *C. adisi* the number of migratory juveniles caught in arboreal photo-eclectors was higher during periods of less insolation (February-May 1977: $p < 0.01$, $r = -0.9914$, $n = 4$; cf. Fig. 4). This was also reported for trunk ascending adults of *Hanseniella arborea*, a migrating symphylan in seasonal mixed- and blackwater inundation forests (ADIS *et al.*, this volume). During rainy seasons which showed an approximately equal amount of precipitation between months and a steady increase of flood waters in the study area, trunk ascents of *C. adisi* occurred over a long period of time, e.g. from December to April in 1983/84. They were relatively short in duration during rainy seasons which were marked by a greater amount of rainfall in certain months and by fast rising flood waters, e.g. in February/March 1976 and in April/May 1983. These two years were characterized by macroclimatic El Niño-Southern Oscillation (ENSO) events (strong in 1982/83 and weaker in 1976/77), which were statistically shown to cause a decrease in total precipitation during the rainy season in Central Amazonia and a lower average water-level of the Rio Negro seven months after the event had begun (ADIS & LATIF, 1995; cf. ROPELEWSKI & HALPERT, 1987; PHILANDER, 1983; RICHEY *et al.*, 1989).

Source : MNHN, Paris

From December 1982 until May 1983 (Fig. 5) the trunk ascent in *C. adisi* was significantly correlated with the rising water gauge of the Rio Negro at Manaus ($p < 0.05$, $r = +0.8380$; $n = 6$).

C. adisi is believed to be nocturnal as it was found to pass the flood period aggregated under loose bark of trunks during the day. The number of specimens caught on individual trees of the same and of different tree species varied considerably (cf. Table 1) and tree trunks with smooth and/or thin bark may be avoided (e.g. *Mora paraensis*). In 1977, trunk descents were observed to occur within 1-2 weeks and at the time when the forest floor was about to emerge from the receding floodwater (cf. Fig. 4).

C. adisi was neither detected in tree crowns (by means of canopy fogging) nor in epiphytes (5-25 m above ground), nor was it found in flooded soils which were taken from under the water during forest inundation. Adults and early juvenile stages occurred solely on the forest floor. Based on the characteristics outlined, *C. adisi* represents a terricolous, migrating and univoltine species, which is considered endemic of seasonal blackwater inundation forests in the Rio Negro valley. Vertical migration of advanced juvenile stages represents an ethological adaptation to escape annual long-term flooding, which was not found in Polydesmida and other terrestrial invertebrates of neighbouring non-flooded upland forests (cf. ADIS, 1992a; GOLOVATCH, 1992a, b).

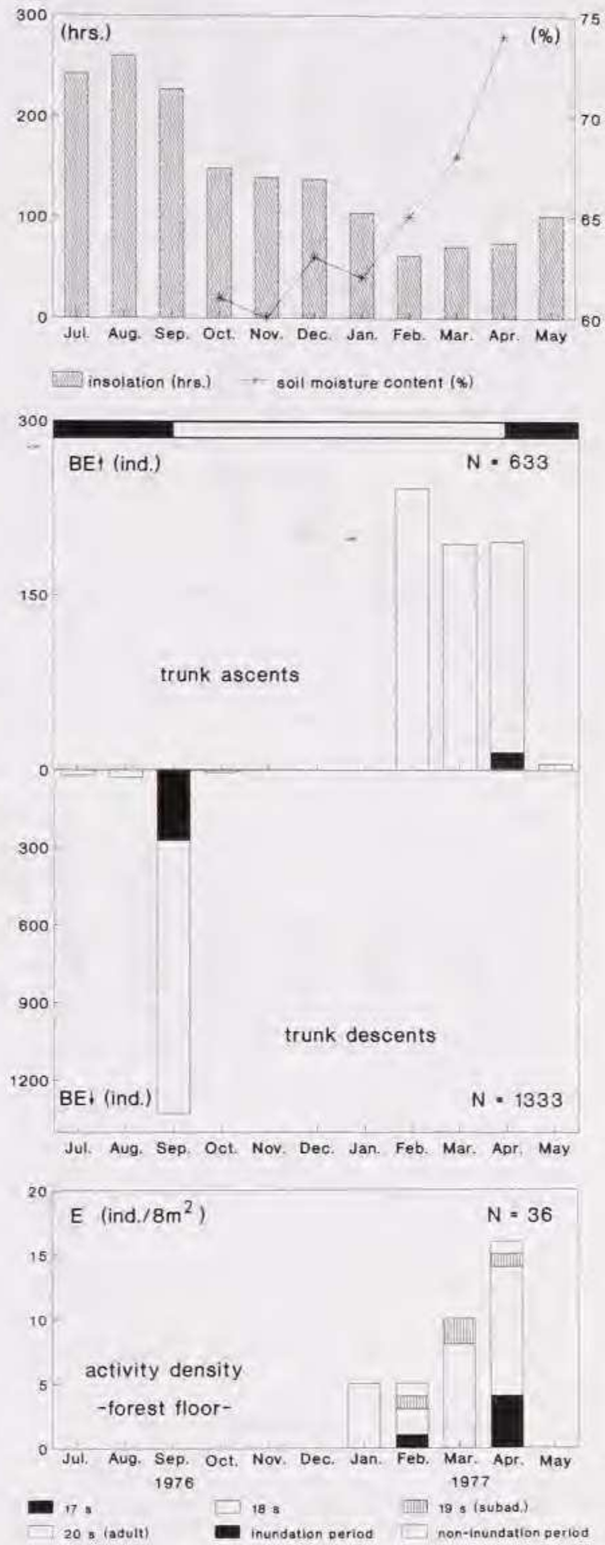

FIG. 4. — Activity density of *Cutervodesmus adisi* on the forest floor (8 ground photo-eclectors (E); ind./8m2), trunk descents (BE↓)and trunk ascents (BE↑); three arboreal photo-eclectors, respectively between July, 1976 and May, 1977 at Rio Tarumã Mirím. Soil moisture content is expressed as the percentage portion of the soil humidity (vol. %) at the maximal water capacity of the soil (= 34 vol. %; cf. ADIS, 1981).

Source : MNHN, Paris

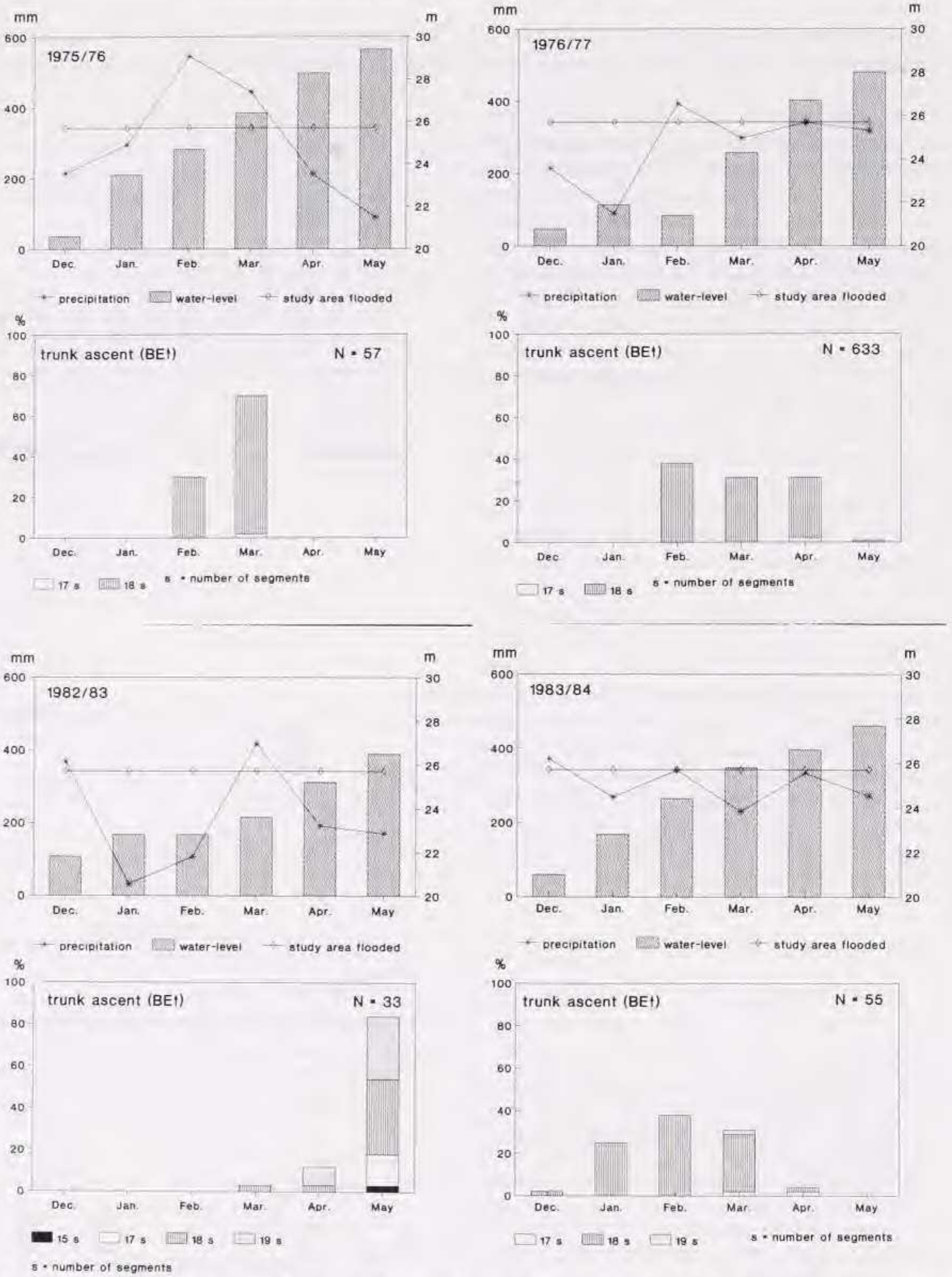

FIG. 5. — Percentage of developmental stages of *Cutervodesmus adisi* ascending trunks caught per month in arboreal photo-eclectors during four rainy seasons in relation to water-level of the Rio Negro and precipitation in the Manaus area; total catch per season = 100 %. (See left page).

Source : MNHN, Paris

The flood pulse is regarded as the original determinant of the upward and downward migrations of terrestrial invertebrates on tree trunks in the seasonal inundation forests of Central Amazonia (ADIS, 1992a). However, it is still the primary control mechanism or ecofactor only among certain species. Most of the invertebrates, like *C. adisi*, have apparently become sensitive to secondary, mainly abiotic ecofactors, which are no longer directly related to the cycle of flooding. The migration of animals from the ground to tree trunks (and their flight to upland forests) is triggered mainly by the rainy season (December - May), which begins three to four months before the flooding, and by the changes in the edaphic and climatic factor it causes.

Following GOLOVATCH's (1987) proposed division of the Diplopoda into morphotypes and ecomorphotypes (= life-forms), *C. adisi* represents a good climber: its body is fairly small (up to 6 mm in length with females being larger (5.0-6.0 mm) than males (4.5-5.3 mm)), the paraterga are relatively small, the legs relatively strong and not too slender, with the somewhat pretarsal podomeres and more slender and long tarsi each crowned with a well-developed claw. Such a morphological pattern also fits a soil dweller (= edaphobiont), which is also the case. The high number of migratory stages (which represented almost half the population in the soil), the probable predominance of females on the forest floor and the synchronization of reproduction in the soil with the non-inundation period compensates for the decline in population density during flooding and assures the persistence of this species in a harsh environment.

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